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POPULATION HETEROGENEITY IN THE PACIFIC PILCHARD

BY FRANCES E. FELIN

FISHERY BULLETIN 86

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

The possibility of heterogeneity in stocks of *Sardinops caerulea* along the Pacific coast of the United States and Canada is examined through evidence from growth and vital statistics of the fished population(s). Growth characteristics of six year-classes sampled in Canada are compared with those from San Pedro. Significant difference in predicted size indicates lack of homogeneity in populations of adults as sampled by the fishery in Canada and in San Pedro.

Evidence from qualitative and quantitative differences in individual scale and growth patterns indicates some independence in the fished stock of the Pacific Northwest and southern California.

Bimodality in length composition of certain year classes is evidence that pilchard populations are not homogeneous. Large, long-ranging pilchard may arise from spawning stocks off California while more southern stocks, smaller in size, more short-lived, have limited migration.

In view of indications of heterogeneity in growth types of fished stocks of pilchard, whether genotypic or phenotypic in origin, it appears desirable that their population dynamics be studied not only for the coast as a whole but also by geographic areas.

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
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POPULATION HETEROGENEITY IN THE PACIFIC PILCHARD

By Frances E. Felin, *Fishery Research Biologist*

the course of routine examination of scales
ne Pacific pilchard (*Sardinops caerulea*) sev-
investigators working together had for a long
noticed the consistent occurrence of dis-
tively small individuals among the 5-year olds.
suggested the possibility that this species
nt be composed of more than one population,
having common and genetically distinct
butes. One of these attributes appeared to
growth rate; others might include habits,
ribution, anatomy, and physiology. Possibly
these populations would have differing rates
birth and death. If this hypothesis should
e true, then the characteristics of each
ulation must be taken into account in any
y involving population dynamics.

o examine the proposition that the species
linops caerulea is a complex of different
ulations, distinguishable by peculiarities in
rth rate, we undertook an intensive study of
growth characteristics as recorded on pilchard
es, and we analyzed these data in the light of
ain pertinent vital statistics. The following
er is a report of that study.

he materials for this study are scales, and age
length data from pilchard sampled by State
Federal agencies. These were collected in as
ly random a fashion as possible from the
hes at major ports along the Pacific coast
re fishing was carried on during each fishing
on from 1941–42 through 1949–50. Since
dation of scale-reading techniques for Pacific
nard (Walford and Mosher 1943a and 1943b),
age and length composition of these samples
e provided the vital statistics from which may
stimated the annual accrual to the stocks by
uitment and growth, and the losses due to
ng and natural mortality and/or unavaila-
y of fish to the fishery.

he assistance of the Fisheries Research Board
Canada, the Washington Department of
eries, the Oregon Fish Commission, the Cali-
a Department of Fish and Game, and of the
many persons who have made possible the continued cooperative program of sampling the catch, is gratefully acknowledged. I wish also to thank Dr. L. A. Walford, O. E. Sette, and J. C. Marr for their constructive criticism and encouragement; Dr. G. S. Myers, Stanford University, for his review of the manuscript; and T. M. Widrig for his assistance in preparing the statistical data.

AVERAGE GROWTH DATA

Growth curves of a given year class of pilchard may be constructed from the mean observed lengths of that year class in successive seasons (Phillips 1948). Such growth curves fluctuate in level from year to year because of the differential migration of the fish of different size (Clark and Janssen 1945) and age, and because of within-season and between-season variations in distribution of the population. Observed lengths, however, provide a useful check on back calculations of lengths, which are based on the proportionality of growth of scale to growth of fish.

DETERMINING LENGTHS BY THE DIRECT-PROPORTION METHOD

For calculating lengths of pilchard a direct proportionality is tentatively assumed in this study, so that

$$\frac{l_n}{l_t}=\frac{s_n}{s_t}$$

where l is length of fish, s is length of scale, n represents any given age, or annual ring on the scale, and t is total length of fish or scale. The scale, of course, is not formed when the fish is 0 mm. long. The extrapolated curve of the linear regression of fish length on scale length may show for adult fish of a given year class, a positive, a zero, or a negative y-intercept and since the scale cannot be laid down at a minus length of fish, the absolute value of the y-intercept can not be

said to have a biological meaning. Regressions of pilchard length on scale length appear to be satisfactorily described by a linear equation over the range of ages 1- through 5-ring (Landa 1950). When the y-intercept differs significantly from zero, the percentage error in estimated length introduced by the assumption of direct proportionality will, of course, decrease with increasing age.

A variety of factors renders the calculated growth for the first year of life, or to the first ring on the scale, only an approximation. The amount of the first growth increment differs geographically, which is partly explained by the northward shift of spawning as the season progresses. Spawning also continues for some length of time at a given locality. There is consequent inequality in duration of the initial period of growth, so that the length of the first year, from the time spawned until the formation of the first winter annul depends upon the place and date of spawni The time periods represented by the l_1, thus not entirely comparable with those represent by other growth increments (l_n). Furthermo there is least clarity in appearance of the first ri on pilchard scales and greater difficulty in locati it than is found with subsequent annuli, so th less reliability is associated with the mean va of the first growth increment, $\bar{l}_1$.

Average observed lengths at each age of the year classes sampled in the commercial ca over nine seasons in five regions along the Pac coast are given in table 1. The means given each age in each region were obtained by assigni equal weight to each year-class average. Th means were then taken as representative of mean curve of growth for each area of cat (See also Phillips 1948, p. 7.)

TABLE 1.—*Average length of pilchard in the commercial catch of five Pacific-coast areas, by year class and age group*

Year class	1-ring		2-ring		3-ring		4-ring		5-ring		6-ring		7-ring	
	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Av ag len
British Columbia:		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*M*
1934													40	
1935											80	241	12	
1936									237	236	51	244	39	
1937							307	230	92	239	100	246	27	
1938					142	216	104	230	148	239	93	245	45	
1939			255	193	313	215	287	234	204	242	95	247	32	
1940	10	175	84	204	89	226	117	239	67	245	26	250	30	
1941					20	231								
1942			37	195	38	225	10	241	17	250				
1943	14	183	29	211			15	243						
Mean	24	179	405	201	602	223	840	236	765	242	445	246	225	
Pacific Northwest:[1]														
1934													62	
1935											112	242	12	
1936									331	236	53	244	40	
1937							483	229	95	239	104	245	27	
1938					294	215	111	231	164	239	93	245	53	
1939			680	191	390	215	322	233	204	242	122	249	61	
1940	35	166	91	203	101	225	117	239	86	247	83	253		
1941	(*)				20	231	(*)		19	253				
1942	(*)		37	195	44	225	22	244						
1943	14	183	29	211	10	236								
1944	(*)													
Mean	49	174	837	200	859	224	1,055	235	899	243	567	246	255	
San Francisco:														
1935											(*)		12	
1936									44	220	86	231	33	
1937							186	217	256	227	93	239	132	
1938					862	209	736	222	348	232	403	244	28	
1939			1,186	199	1,346	216	959	228	896	241	55	247	12	
1940	21	180	205	208	574	223	665	236	78	240	(*)			
1941	(*)		51	206	185	223	80	222	(*)					
1942	48	173	313	212	191	222	16	238						
1943	46	182	147	210	13	234								
1944	(*)		14	209										
1945	18	168												
Mean	133	176	1,916	207	3,171	221	2,642	227	1,622	232	637	240	217	

See footnotes at end of table.

LE 1.—*Average length of pilchard in the commercial catch of five Pacific-coast areas, by year class and age group*—Con.

Year class	1-ring		2-ring		3-ring		4-ring		5-ring		6-ring		7-ring	
	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length
erey:		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
935											(*)		11	232
936									36	218	55	231	18	237
937							164	215	161	229	98	235	44	245
938					903	206	700	220	367	230	163	242	15	247
939			2,487	195	1,684	214	1,167	226	537	239	58	247	16	254
940	447	175	641	205	949	221	470	234	71	236	21	243		
941	137	164	255	198	352	219	150	219	43	237				
942	570	164	1,379	204	320	219	77	234						
943	450	170	255	209	135	232								
944	73	172	83	207										
945	324	184												
Mean	2,001	172	5,100	203	4,343	218	2,728	225	1,215	232	395	240	104	243
Pedro:														
935											11	223		
936									43	212	15	215		
937							140	212	58	214	22	223		
938					1,090	202	448	210	97	219	31	231		
939			1,756	194	1,301	206	443	213	178	224	14	224		
940	419	179	1,373	198	834	206	415	213	44	218	(*)			
941	476	181	1,112	196	1,141	206	151	213	26	222	11	237		
942	485	180	1,060	204	242	206	59	220	45	237	(*)			
943	546	187	337	200	186	213	83	228	9	219	(*)			
944	105	182	283	205	161	219	33	213	28	212				
945	397	195	281	210	99	210	61	208						
946	195	169	407	199	210	206								
947	59	187	253	198										
948	75	189												
Mean	2,757	183	6,862	200	5,264	208	1,833	214	528	220	104	226		

Includes samples from waters off Washington and Oregon.
Less than 10 fish sampled.

TRANSFORMATION OF GROWTH CURVES

When such growth curves of means-of-average erved lengths for each area are transformed, ng Walford's (1946 a) plot of l_{n+1} on l_n, figure 1 ults. These transformations show marked iation from the linearity characteristic of this for more homogeneous groups of fish (or of er animals). They are illustrative, however, growth characteristics of different areas. As ned by Walford, these are (1) the slope of the ression, k, representing the rate of deceleration growth; and (2) the predicted ultimate size, $\frac{y\text{-intercept}}{1-k}$. Pilchard landed at Monterey San Francisco show growth characteristics rmediate between those of catches landed the south at San Pedro and in the Pacific thwest off Oregon, Washington, and British umbia.

rowth data on European pilchard (*Sardina hardus*) assembled from various sources by De n (1937) are plotted similarly (as trans- nations) in figure 2 for different geographical areas. These curves are based on back calculations of length obtained for the most part by the direct-proportion formula. Differing growth types, possibly representing clines (or gradients) of growth, are indicated from north to south, extending from waters off England through the southern European Atlantic to the Mediterranean. In figure 2, solid symbols represent transformations of growth curves of pilchard off Cornwall, Plymouth, and Northumberland; various crosses and parts of crosses show growth transformations of pilchard from the English Channel off Boulogne, from other waters south along the French and Spanish coasts as far as Cadiz and the Azores; and open symbols represent pilchard growth types from the Mediterranean. As early as 1913 Fage suggested, on the evidence of growth, that two distinct races of sardines exist, one in the Atlantic and another in the Mediterranean. He also noted (1920) that the relative dwarfism of Mediterranean races is not peculiar to the sardine, but has also been noticed in the anchovy and other species common to the two seas.

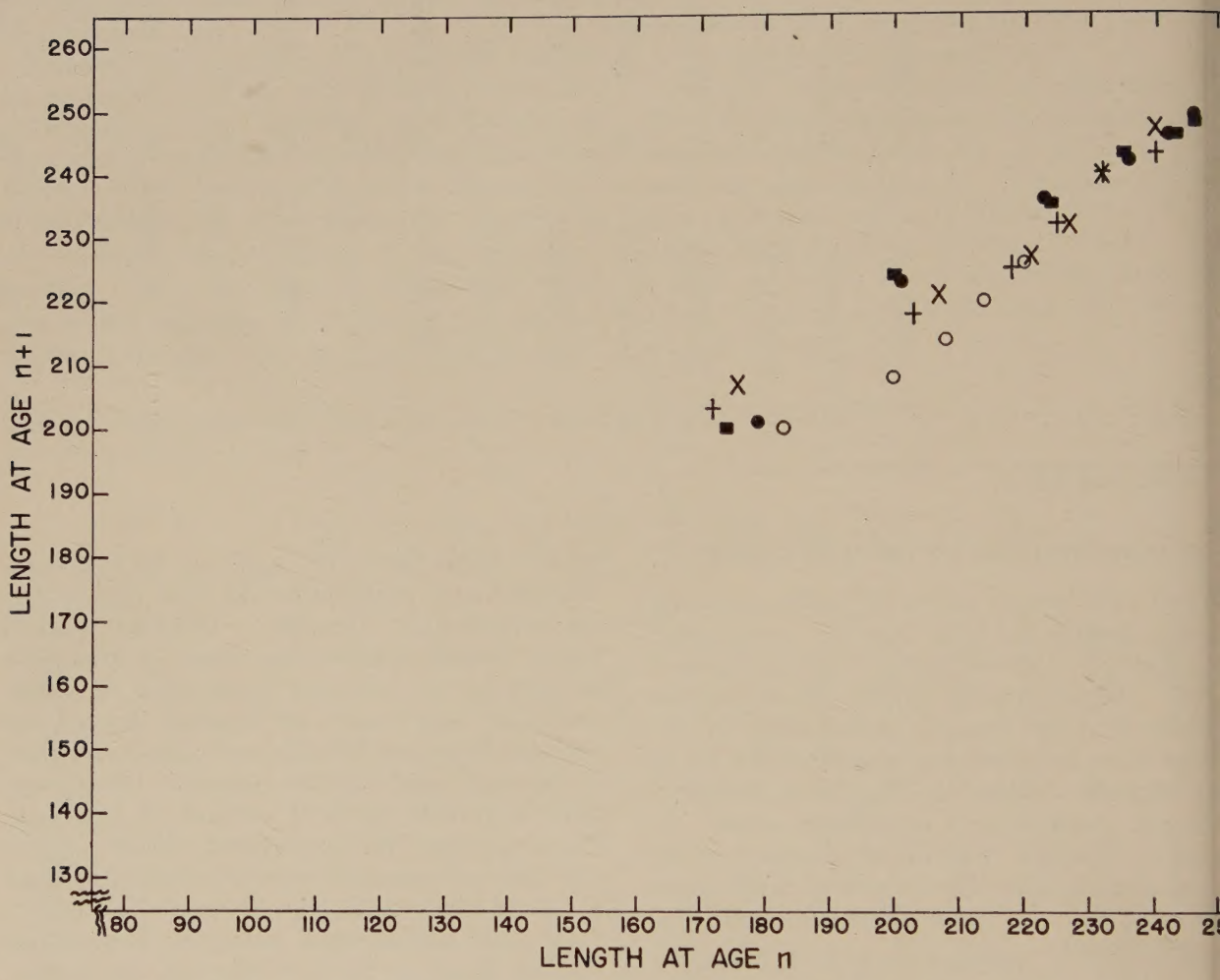
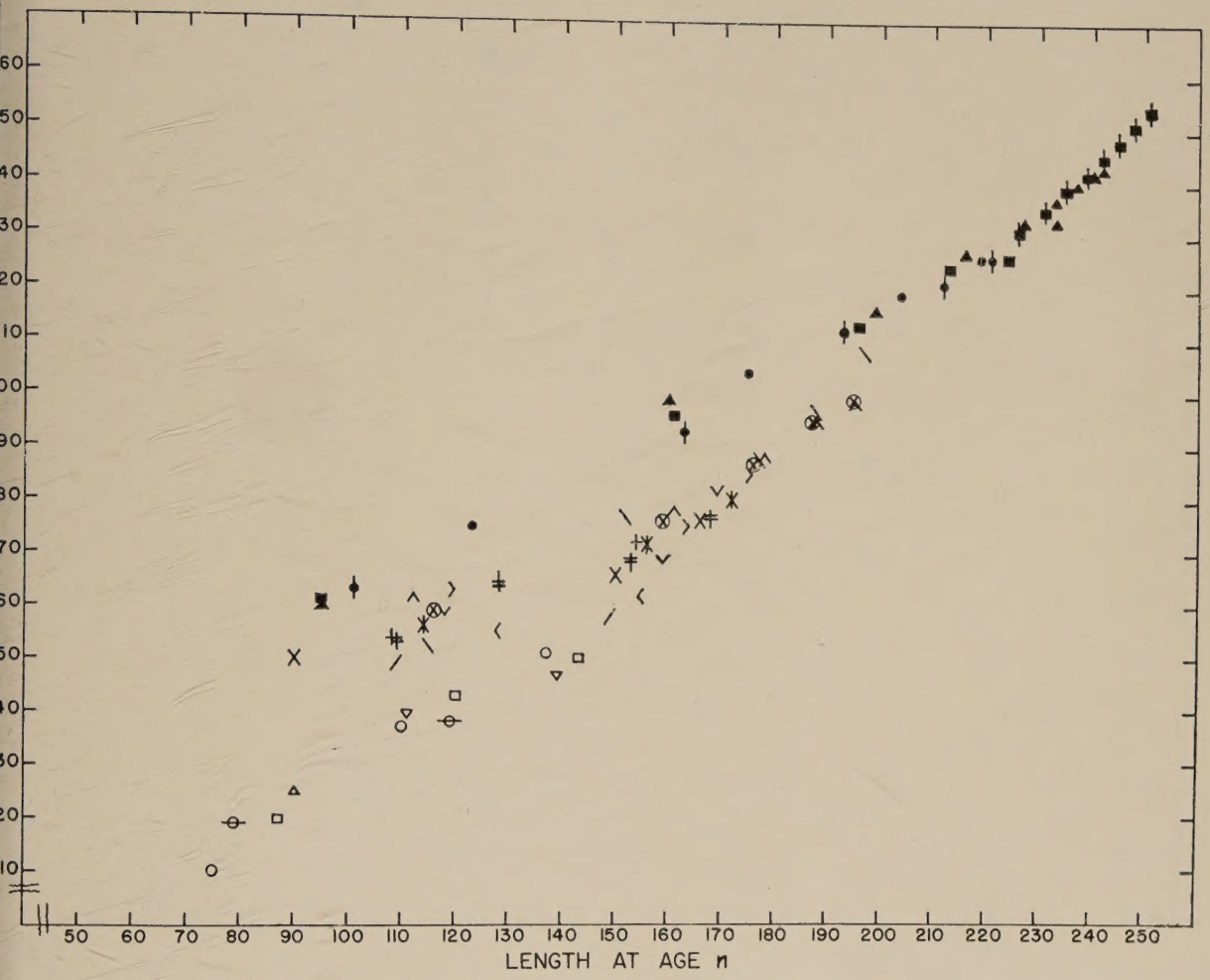


FIGURE 1.—Transformations of 9-season averages of observed lengths of Pacific pilchard at each age in five region catch. British Columbia averages represented by dot, Pacific Northwest by solid square, San Francisco by cr Monterey by plus, San Pedro by circle.



URE 2.—Transformations of growth curves of European pilchard from different regions of catch. Solid symbols represent pilchard caught off England, various crosses and parts of crosses those off the French and Spanish coasts, open symbols those from the Mediterranean. (Data from De Buen 1937.)

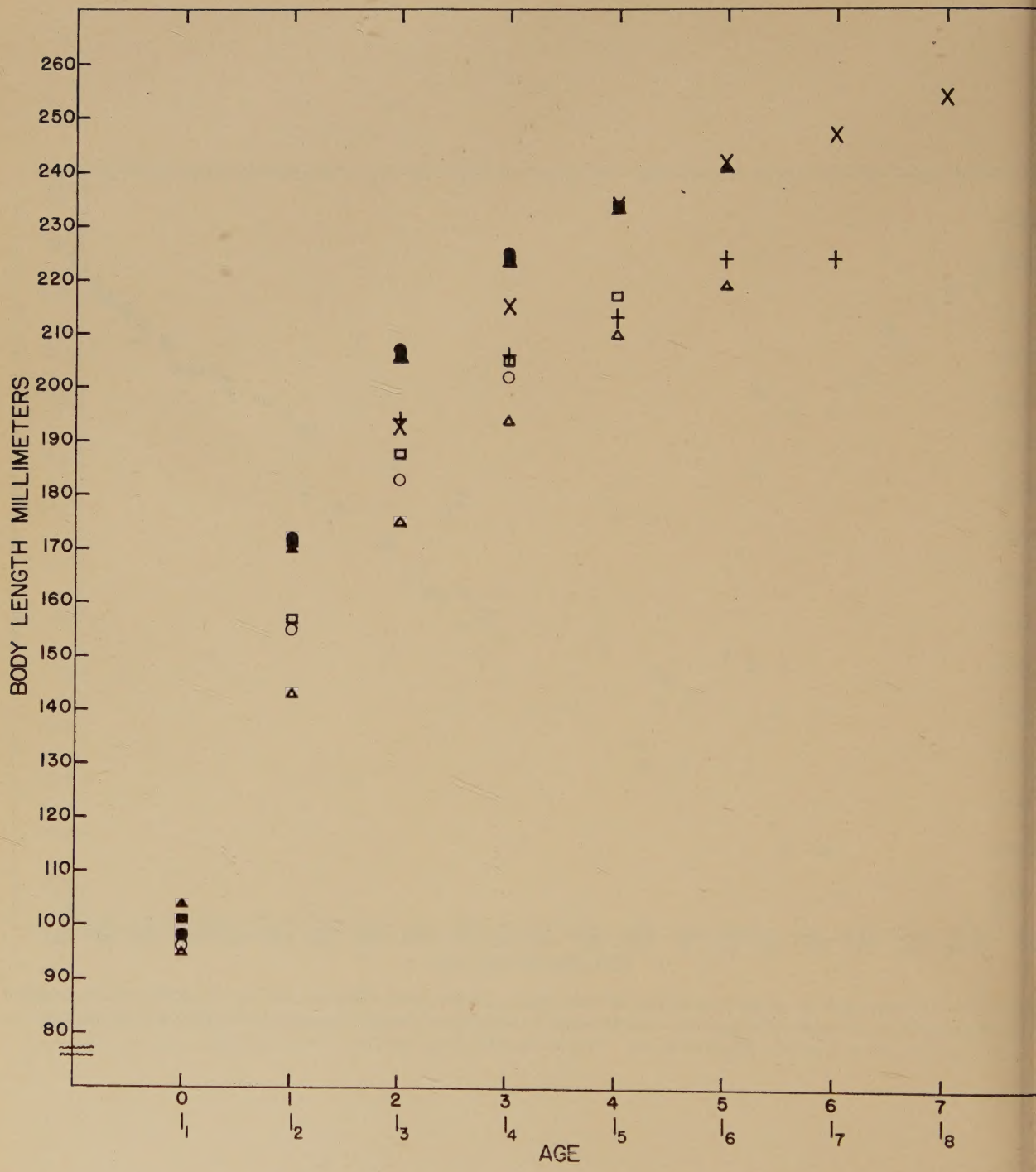


FIGURE 3.—Growth of pilchard of the 1939 year class taken in Canada and in San Pedro. Mean observed lengths fish taken in Canada are shown by crosses, those in San Pedro by pluses. Mean calculated lengths of 4-, 5- a 6-ring fish are shown by circles, squares, and triangles, solid symbols for Canada, open symbols for San Pedro.

GROWTH CURVES OF 1939 YEAR CLASS

[tilizing mean calculated lengths (table 2) for a
en year class of Pacific pilchard taken in the
t northern region of catch, Canada, and in
most southern, San Pedro, we may compare
wth curves derived from mean calculated
gths with those derived from mean observed
gths for each year class throughout its life in
fishery. An advantage in the transformation
t is graphically illustrated by figures 3 and 4.
s not readily apparent from the conventional
wth curves of the 1939 year class (fig. 3) that the crosses delineating the growth curves derived from mean observed lengths of the year class in successive seasons express the same rate of deceleration of growth as do the mean back calculations of length for 4-ring, 5-ring and 6-ring fish (circles, squares, and triangles) of this 1939 year class. Solid symbols represent northern calculated-length data, open symbols the southern. These same curves transformed (fig. 4) show the relative constancy of slope (k) as well as level (y-intercept) of the regressions for northern and southern populations, whether plotted from observed or calculated length data.

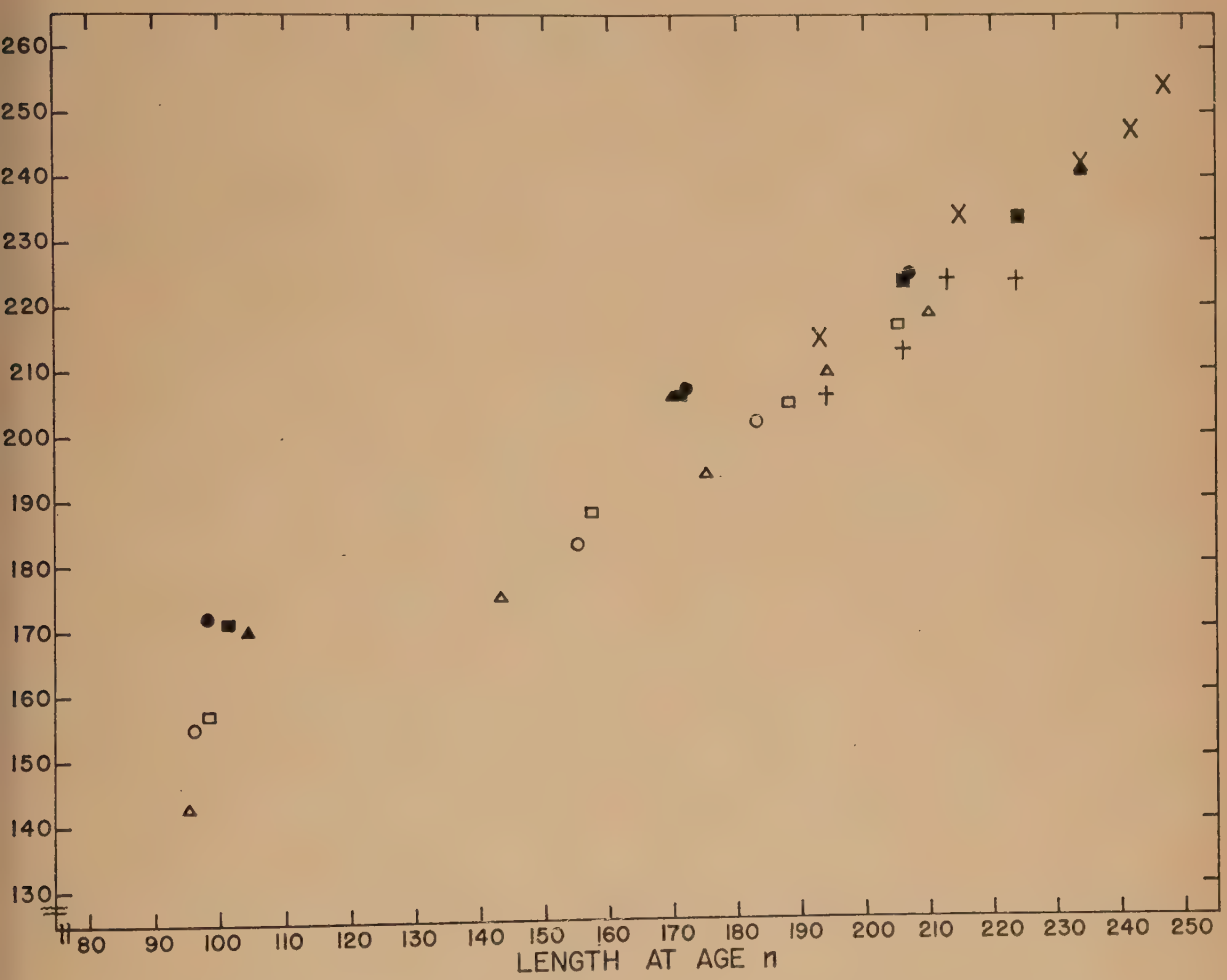


FIGURE 4.—Transformations of the growth curves of the 1939 year class shown in figure 3.

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TABLE 2.—*Average calculated lengths* ($\bar{l}$) *of year classes at 4-ring and older, sampled in the commercial catch of pilchard, British Columbia and San Pedro*

[Parentheses indicate average based on 13 5-ring fish from Washington brackets, fish from Oregon; asterisks, 9 fish sampled]

Year class and calculated length ($\bar{l}$)	British Columbia			San Pedro		
	4-ring	5-ring	6-ring	4-ring	5-ring	6-ring
1937:						
$\bar{l}_1$	118	113	112	105	102	109
$\bar{l}_2$	175	173	172	161	156	161
$\bar{l}_3$	206	208	205	192	184	187
$\bar{l}_4$	223	225	223	205	197	202
$\bar{l}_5$	----------	236	234	----------	207	211
$\bar{l}_6$	----------	----------	241	----------	----------	218
1938:						
$\bar{l}_1$	103	107	110	96	98	103
$\bar{l}_2$	169	173	172	162	161	161
$\bar{l}_3$	203	206	205	188	188	191
$\bar{l}_4$	218	222	222	201	201	208
$\bar{l}_5$	----------	232	233	----------	211	217
$\bar{l}_6$	----------	----------	240	----------	----------	225
1939:						
$\bar{l}_1$	98	101	104	96	98	95
$\bar{l}_2$	172	171	170	155	157	143
$\bar{l}_3$	207	206	206	183	188	175
$\bar{l}_4$	225	224	224	202	205	194
$\bar{l}_5$	----------	234	234	----------	217	210
$\bar{l}_6$	----------	----------	241	----------	----------	219
1940:						
$\bar{l}_1$	108	112	112	103	105	----------
$\bar{l}_2$	179	178	182	156	158	----------
$\bar{l}_3$	213	211	211	185	184	----------
$\bar{l}_4$	230	228	227	202	200	----------
$\bar{l}_5$	----------	238	238	----------	211	----------
$\bar{l}_6$	----------	----------	246	----------	----------	----------
1941:						
$\bar{l}_1$	----------	(116)	[112]	100	107	----------
$\bar{l}_2$	----------	(186)	[179]	156	166	----------
$\bar{l}_3$	----------	(219)	[214]	187	195	----------
$\bar{l}_4$	----------	(236)	[231]	204	207	----------
$\bar{l}_5$	----------	(248)	[241]	----------	216	----------
$\bar{l}_6$	----------	----------	[248]	----------	----------	----------
1942:						
$\bar{l}_1$	107	95	[108]	116	109	----------
$\bar{l}_2$	183	166	[170]	174	170	----------
$\bar{l}_3$	213	211	[208]	198	203	----------
$\bar{l}_4$	232	231	[230]	211	219	----------
$\bar{l}_5$	----------	242	[244]	----------	230	----------
$\bar{l}_6$	----------	----------	[254]	----------	----------	----------
1943:						
$\bar{l}_1$	111	[112]	----------	115	*116	----------
$\bar{l}_2$	172	[177]	----------	174	*163	----------
$\bar{l}_3$	205	[213]	----------	203	*190	----------
$\bar{l}_4$	229	[234]	----------	218	*202	----------
$\bar{l}_5$	----------	[247]	----------	----------	*211	----
1944:						
$\bar{l}_1$	[129]	----------	----------	133	130	----------
$\bar{l}_2$	[196]	----------	----------	175	169	----------
$\bar{l}_3$	[228]	----------	----------	193	185	----
$\bar{l}_4$	[246]	----------	----------	205	197	----------
$\bar{l}_5$	----------	----------	----------	----------	207	----

CONSISTENCY OF GROWTH CURVES

Year classes 1937 through 1942 provide sufficient data for construction of curves of growth similar to those of the 1939 class (see tables 1 and 2). For the year classes 1937 through 1940, the estimates of means have greater reliability owi to more extensive sampling during seasons 1941–4 through 1944–45. A decline in catches coincide with curtailment of the sampling program so th from seasons 1945–46 through 1949–50 the est mates of mean lengths are based on fewer fish.

The transformations for year classes 1937, 193 1940, 1941, and 1942 are similar in growth cha acteristics to those of the 1939 year class (s table 3). From analysis of covariance, no signif cant difference was apparent in the mean slope k, of the transformations between each of thes year classes in the two areas of catch, Canada an San Pedro. That slope, or rate of deceleration growth, is the more stable of the two growth cha acteristics, and that, with relatively constant en vironments, slope is a physiological character genetic meaning, is suggested from an exper mental study of growth in *Platypoecilus maculat* (Felin 1951).

For each of the year classes tested, two distinc y-intercepts, or levels, for transformations of mea calculated and observed lengths are maintained i the northern and southern areas. From the c variance tests, the differences are significant a the 1-percent level. Further translated into pre dicted ultimate size $\left(\frac{y\text{-intercept}}{1-k}=l_\infty\right)$, the rang of the means for San Pedro is 220–236 millimeter standard length, and for Canada, 249–258 mill meters, with no overlap for those year classe tested (table 3).

TABLE 3.—*Growth characteristics in northern and souther areas of catch derived from regressions of means* l_{n+1} on

Year classes	Rate of deceleration, slope (k)		y-intercept levels		Ultimate size (mm $\left(l_\infty=\frac{y\text{-intercept}}{1-k}\right)$	
	British Columbia	San Pedro	British Columbia	San Pedro	British Columbia	San Pedro
1937	0.57	0.54	108	102	251	2
1938	.55	.52	112	107	249	2
1939	.54	.59	115	94	250	2
1940	.52	.55	120	99	250	2
1941	.52	.56	123	101	256	2
1942	.53	.53	121	111	258	2

BIOLOGICAL SIGNIFICANCE OF DIFFERENCE I GROWTH CHARACTERISTICS

Significant difference in level, or the growt characteristic l_∞, may represent phenotypic re sponse of a plastic genotype to varying hydro graphic environments. It may be useful as a

dicator, as suggested for vertebral counts in uropean pilchard (Ruivo 1950) to separate mogeneous populations of certain fishing areas thout implying genetic significance. The re-lts of the covariance tests apply only to mean owth curves, and at present it seems probable at if significant difference were found in the owth characteristic k in certain individuals or gments of the population it would indicate notypic difference.

There is some evidence that deviations from e straight-line regression for each area are eater for mean observed lengths of a year class successive seasons of catch than for mean lculated lengths of a year class in one season. o compare transformations of mean observed ngths with those of mean calculated lengths is ther difficult since observed lengths are not tained until the scales have one ring, or the fish e in their second year of life, when they have complished much of their growth; whereas, lculated lengths begin at 1-ring, and this first owth increment as already noted shows great riability. In San Pedro growth curves for e 1942 class, however, variance of mean observed ngths alone about the regression is 10 times the riance for calculated lengths only. Such ir-gularities suggest that greater shifts in popula-ons of a given year class may occur from season season than within one season. Small devia-ons from the transformations of mean calculated ngths of the 4-, 5- and 6-ring pilchard of each ar class indicate that within a single fishing ason the populations at each port are more mogeneous.

rth-south migration of larger fish

Tagging of fish along the Pacific coast by some the agencies engaged in pilchard research ves evidence of extensive migrations (Hart 43a). It is the larger fish within a group tagged the south that are caught first farthest to the rth (Clark and Janssen 1945, pp. 19–20). iat some of the larger pilchard cover great stances is likewise indicated in the apparent ift at older ages in central California and San dro toward the level of regression of northern owth types as shown in transformations of the ear averages of observed lengths (fig. 1).

If, however, the migration course for the entire pulation were of great seasonal regularity from south to north and return, one would expect with increasing age of fish a tendency toward homogeneity of growth types along the coast. If populations of older fish became more homogeneous in their growth characteristics, a given year class at 5- or 6-rings would show a tendency for the level of northern and southern growth types to shift toward a single norm of oceanic migratory sardines common to all areas of the fishery, or at least to shift toward a level and slope other than the one consistently associated with a particular area of catch. This shift does not so far occur in transformations of mean calculated length data. At 4-, 5-, and 6-rings the levels of these regressions remain distinct for northern and southern sardines (*cf.* fig. 4).

Complete intermixture and homogeneity in populations of adult pilchard in different regions of catch is not evidenced from available data on mean calculated lengths. The distinct levels of the growth transformations which are maintained in northern and southern populations, however, do not controvert the evidence from tagging that there is migration of larger fish toward the north. As is shown from tagging results, growth data also indicate migration of northern pilchard into southern waters. That larger fish of older ages enter the southern catches is demonstrated not only from the 9-year averages of observed length data (fig. 1), but likewise for a single year class as it passes through the fishery (*cf.* table 1). For San Pedro the increase in mean observed lengths for certain individual year classes at 5-ring and older is reflected in a sharp rise at this stage in their length-on-time curves of growth. Similarly, an apparent departure from an expected asymptote of length is observable in Phillips' (1948, p. 7) curve of average observed length of sardines at each age over a 6-year period at San Pedro. Such irregularity in the San Pedro growth curves must be explained by an influx onto southern fishing grounds of large, old fish differing in their growth pattern from the smaller fish up to 4-ring age which are caught in San Pedro. Conversely, in certain other year classes, there has been an actual decrease in observed lengths as a year class reached older ages and was caught off San Pedro. This indicates an influx of smaller fish of more southern growth characteristics onto these grounds. The extent of the seasonal north-south migration and the

extent of season-to-season variability in interchange of northern and southern populations are as yet not determined.

Possibilities of inshore-offshore migrations of pilchard are in the main unexplored and, short of the use of radioactive markers, may be difficult to determine. Hart (1943a, p. 178), however, records tagged fish moving into inlets on the west coast of Vancouver Island and remaining there throughout the winter. Such winter fish, according to Hart, "are occasionally captured during the winter herring fishing season and . . . they sometimes provide early in-shore fishing before the main pilchard shoals approach the Vancouver Island coast in the summer."

North-south variation in growth characteristics

The variation in growth of pilchard from north to south may prove to be a physiological characteristic of clinal significance. The study of intraspecific clines in fishes is, of course, complicated by what Mayr (1944, p. 135) terms the "strong and only rather recently appreciated phenotypical plasticity of many species." It seems likely that the greater size of fish in northern waters is not entirely explained by northern migration of the larger individuals of each year group. These northern pilchard may represent a separate stock grown to larger sizes rather than only a sorting out of larger fish from a whole coastal population. It may be that such growth differences from north to south can be explained in part by geographical gradients in environmental factors associated with gradients in morphological and physiological characters, or clines, within the range of a species.

It seems probable from existing evidence on growth characteristics of the fish in different geographical regions that there may be season-to-season fluctuations in the size and the location of optimum living areas associated with fluctuations in marine climate. Such fluctuations may largely determine what part of the sardine population will be available for capture in each area. Illustrative of between-season shifts in populations are the apparently greater deviations in mean observed lengths than in mean calculated lengths of a year class from its rectilinear transformation. But it also seems evident from back calculated lengths that there is, for a given year class, a persistent cline in growth characteristics from north to south, and that populations, although fluct ating in distribution from season to season ar somewhat migrant, may be more discrete ar limited latitudinally than has been supposed fro the evidence of vertebral counts (Clark 193 1947) and tagging (Hart 1943a; Clark ar Janssen 1945).

McHugh (1950) has reported on latitudin variation in three species of clupeoids of the Nort Pacific. Parallel gradients in hydrographic an meristic characters and consequent homogeneit or heterogeneity of populations with respect t certain characters are discussed. For the nortl ern anchovy (*Engraulis mordax*) and Pacific sa dine, McHugh found clines in anal fin-ray coun and significant heterogeneity among several po ulations. He notes close parallelism in meristi counts of anal fin rays in anchovy and sardine and likewise in vertebral counts of both specie From his more complete study of meristic cha acters in anchovy, McHugh concludes (p. 58) tha "clines in numbers of dorsal, anal and pectora fin rays are in the opposite direction to ths shown for gill-rakers, and all four fail to corre spond with the distribution of mean vertebra number."

McHugh considers it probable that in the Pa cific Northwest the fixation period for sardin fin-ray counts occurs during a period of warme water temperatures, while in southern Californi water temperatures average lower at this perio of development. Thus the usual inverse relatio between meristic count and temperature follow for counts of fin rays as well as of gill rakers, an to a lesser degree of vertebrae.

Lack of significant differences in vertebra counts between samples of sardines from Britis Columbia to southern California (Clark 193 1947), and the heterogeneity in populations ac cording to fin-ray counts, McHugh attributes t close dependence of each meristic character o coexistent physical factors in the environment a the time of fixation of the character. Since spawn ing occurs within a rather narrow temperatur range, phenotypic variation could likewise be nar row for a character, such as vertebral numbe with an early fixation period, whereas with a late perhaps longer, fixation period there could b greater concomitant variability in environmenta factors and heterogeneity of populations as ind cated by these other meristic characters.

McHugh's results on vertebral counts thus agree
h Clark's; and he concludes (p. 110)—

ince the number of vertebrae drops very sharply with
reasing latitude off Baja California, it is assumed that
se fish belong to a distinct race that has different tem-
ature requirements.[1] It is also concluded that the
nber of vertebrae is not a particularly critical measure
opulation segregation in pelagic spawning species.

McHugh further suggests that—

rmingling between populations may not be random
h respect to meristic or other characters. If this
o, wandering of individuals, as shown by tag returns,
y not necessarily indicate movements of the population
a whole. Experimental verification of these deductions
nuch needed . . .

The apparent cline in growth characteristics
ggests the presence of intraspecific populations
which there is limited intermingling. Rather
an a general coastwise migration pattern, a
ies of overlapping coastal migrations of more
an one stock appears more consonant with
served data on growth.

owth characteristics determined by origin

There is increasing reason to suppose that the
ographic origin of sardine populations may be
dely variable from season to season. Evidence
om spawning studies demonstrates that there
re, during 1949 and 1950, two centers of
awning; one, early in the year, around and to
e south of Cedros Island off central Lower
alifornia, and another, somewhat later and
rther offshore, off southern California. It is
so reported (California Cooperative Sardine Re-
arch Program 1950, p. 37) that "In the waters
parating these two spawning centers very little
awning has been encountered during either
ason, and this little has been confined to a
astal strip . . ." During these two seasons
ere was little indication of northern spawning.
1940, however, an unusual abundance of young
h of the 1939 year class was reported (Walford
d Mosher 1941) in north Pacific waters off
regon, Washington, and British Columbia. The
obable occurrence of northern spawnings of
sser magnitude is suggested by the presence in
her seasons of small, presumably 1-ring,
lchard in British Columbia waters recorded
by Hart (1943b). The growth characteristics of northern and southern populations may thus be early determined by their origins.

Whether the populations sampled by northern and southern fisheries have genetically distinct components has not been demonstrated. The significantly different levels of their mean growth transformations may indicate only phenotypic differences in growth ascribable to differing environmental conditions at time and place of spawning or in later life or both. These differing conditions of growth must largely be maintained, however, in each area and in each population sampled, since the mean levels of growth transformations characteristic of each geographic region have remained relatively constant and distinct as shown from calculated length data for 4-, 5-, and 6-ring sardines of each of six year-classes over the seasons of study. This appears to point to the conclusion that there may be a southern spawning center which contributes more heavily to the southern California stocks and that although some of the more southern growth types migrate into central California, they are found rarely in the Pacific Northwest.

The existence of an area of intense spawning off central Lower California was not realized until the expanded sardine research program under the California Marine Research Committee made possible the collection of eggs and larvae in this spawning center as well as in the better known area of more widespread spawning off southern California. In both areas, times of spawning vary between seasons and appear to be associated with conditions of favorable temperature and upwelling. (See California Cooperative Sardine Research Program 1950, p. 39.) The varying importance of the contributions of the two areas to the present sardine fisheries is suggested in differing prevalence of southern or of northern growth types in the catches. It appears to be a reasonable hypothesis that the spawning grounds off central Lower California give rise to the southern components found in the catches off San Pedro (and to a lesser degree in catches off central California), while the large northern fish originate off southern California and to the north in years favorable for northern spawning. It is not yet known whether spawning populations in the two main centers are or are not distinct, i. e., genetically isolated in space and time.

[1] From data obtained in the California Cooperative Sardine Research
ogram in 1949 and 1950, the spawning requirements, so far as temperature
oncerned, have been closely similar in what at present appear to be the
main centers of spawning (1) off central Lower California and (2) south-
California.

Fish in the northern part of the range of the fishery are perhaps distinguishable as large, long-ranging individuals, while southern stocks may be characterized by smaller size and more limited migration routes. These stocks appear to overlap in their distribution on fishing grounds as evidenced from the length-frequency data accumulated over a long period of years by the California Department of Fish and Game and later by the State agency in cooperation with the United States Fish and Wildlife Service. Over the period of study of age composition of the catch for which length composition by age is also available, it is evident that the smaller sizes of each year class are rarely caught north of central California.

Ronquillo (1949, p. 29) found that the sizes of pilchard in the Pacific Northwest during most months of fishing did not differ significantly from those caught off central California, but that fish from both these regions showed significant differences from those taken off San Pedro. Over three seasons, from 1945–46 through 1947–48, in all age groups there was a significant difference in size between fish landed at San Pedro and Monterey. During the first 2 years of life sardines taken at San Pedro were significantly larger; in older age groups those landed at Monterey were larger than those at San Pedro. Ronquillo (op. cit., p. 25) also found that the coefficient of variation fluctuated more at San Pedro than at other localities which indicated greater heterogeneity in those samples. He found this measure relatively constant in the Pacific Northwest and therefore indicative of homogeneity within the samples.

The tendency for smaller sizes to remain in the southern part of the range of the species is illustrated also by tagging results (Clark and Janssen 1945, p. 22). They found a southward migration of some of the sardines released in central California and note—

> a greater proportion of the smaller sizes have made this southward migration. For the group tagged in 1940, 72 percent of the recoveries in southern California during the first season after tagging were less than 19 cm. when tagged. For the same season in central California only 50 percent of the recoveries were of these smaller sizes. During the second season after tagging, 74 percent of the southern California recoveries were less than 19 cm. when tagged but only 43 percent of the central California recoveries were composed of these smaller sizes.

Recoveries of sardines tagged off central Lower California have been almost entirely in California Approximately 78 percent were recovered i southern California, 15 percent in Monterey, percent in San Francisco and less than half of percent (represented by one tag) in Washingto (Janssen 1948). Concerning the absence o recoveries in Lower California, Janssen (p. 7 states as follows:

> No tag recoveries have been reported from reductio plants in Lower California. Facilities for recovering tag were in operation there for only a brief period and th quantity of sardines processed in Mexico is small in com parison with other localities along the coast.

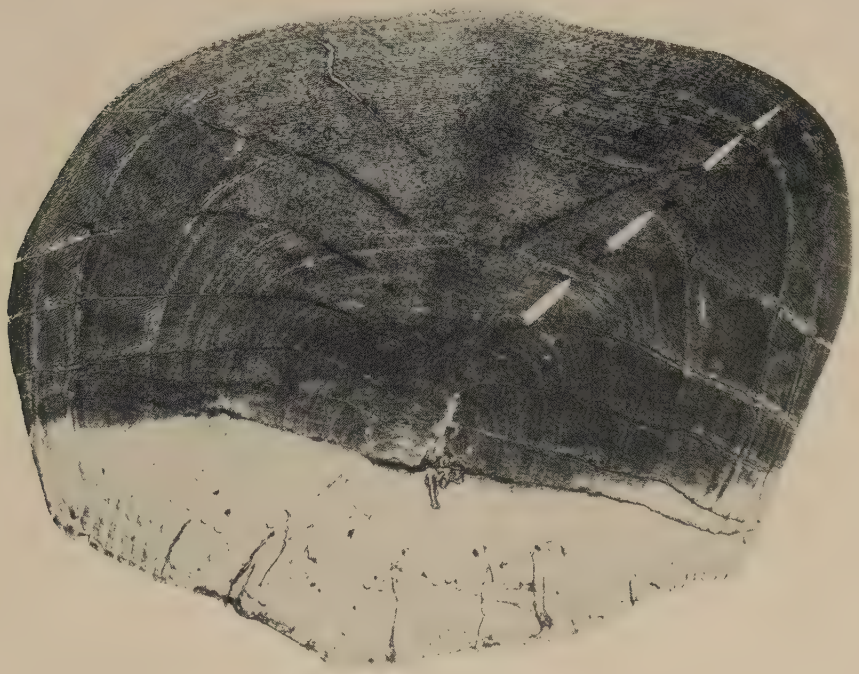
Considering the total number of tags recovere without regard to area of recovery, only 10 per cent of tags put out off Mexico were recovered while off southern California 23 percent and of central California 25 percent were recovere (according to Janssen's adjusted percentage re covery figures, p. 9). The Mexican tagging further indicate the tendency for the southern fis to remain in southern waters.

The larger pilchard of a year class, on the othe hand, commonly are caught on any of the usua fishing grounds from the Pacific Northwest t southern California. Whether the significan difference in attained ultimate size, l_∞, of south ern as opposed to northern growth types arises b reason of primary difference either in location o spawning centers or in location of nursery grounds or both, and whether in turn difference in origi of stocks also represents genetic difference awai further data from spawning studies and determi nation of how discrete are the areas of spawnin and of spawning stocks.

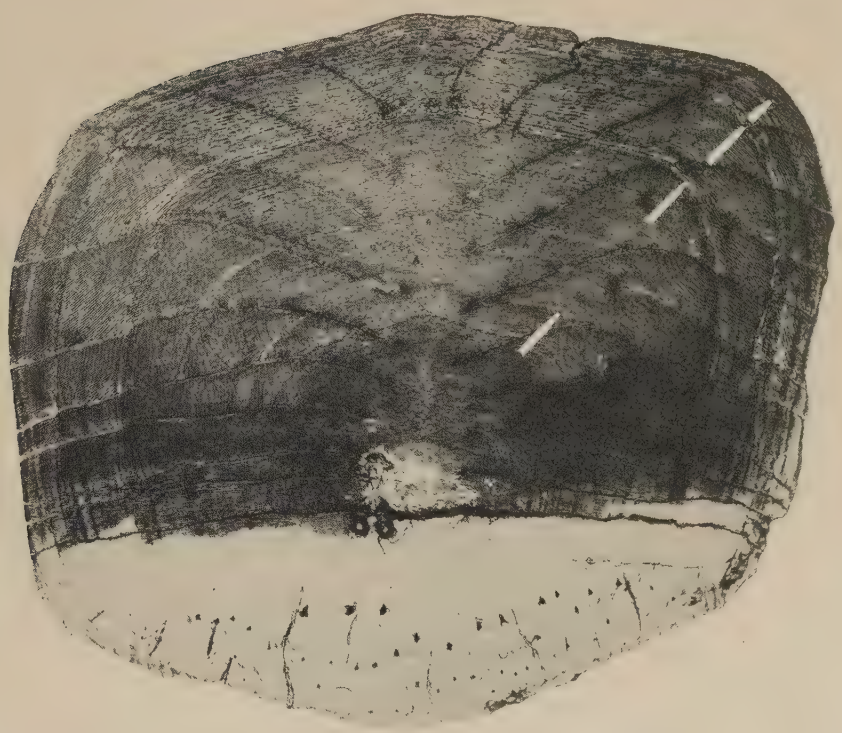
The apparent differences in growth characteris tics in populations along the coast suggest th desirability of study of population dynamics no only for the coast as a whole but also for geo graphic areas, e. g., for the Pacific Northwest central California, southern California, and furthe subdivisions of areas off Lower California not ye clearly delineated.

SCALE AND GROWTH PATTERNS OF INDIVIDUAL FISH

That the fished stocks of the Pacific Northwes and southern California have, for practical pur poses, some independence seems indicated fro further lines of evidence.

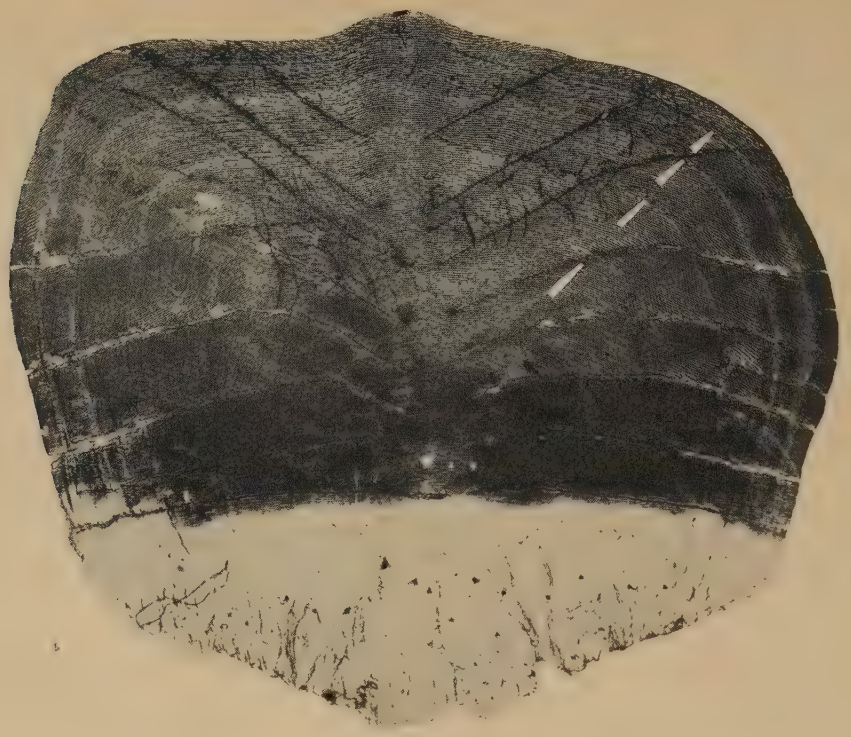


(1) Northern type from Canada (249-mm. female)



(2) Northern type from San Pedro (241-mm. female)

URE 5a.—Growth types of Pacific pilchard at 4-ring stage as shown in scale patterns. These scales show the well-defined annual rings of large fish caught commonly in the north, but also entering the southern fishery. They have a proportionately small first-growth increment and a rapid rate of deceleration in growth.



(3) Southern type from San Pedro (206-mm. male)

(4) Southern type from San Pedro (204-mm. female)

FIGURE 5b.—Growth types of Pacific pilchard at 4-ring stage as shown in scale patterns. These scales show fainter ye marks common among smaller fish in southern catches, rarely caught in the north. The proportionately large firs growth increment is common to both; (3) shows slow deceleration, (4) fast deceleration.

Early in the examination of scales for age ermination, qualitative differences were noticed the scale patterns of pilchard from different ions of catch. An attempt was made to estab- criteria for separating ring types somewhat as l been done in herring by Norwegian investiga- s (Runnstrøm 1936). Although scales collected the Pacific Northwest showed predominantly vily marked winter rings of the northern type ociated with sharp cessation of growth (*cf.* fig. , and those from the San Pedro fishery showed, a rule, the faintly marked annuli suggesting der winters (*cf.* fig. 5b), the presence of inter- diate ring types in central California made the aration too subjective for quantitative treat- nt.

Further attempts to separate the varying growth terns in individual fish were made using trans- mation values (calculated by the method of niaverages) asymptotic length (l_∞) and rate deceleration of growth (k) for individuals ght in four geographical regions. For the 9 class, the regression of the values l_∞ on k e scatter diagrams (fig. 6) for Canada (N=286, s) and San Pedro (N=433, circles). Even ugh there is overlapping in the scatter of ividuals caught in the two areas, a large pro- tion of 4-ring sardines of the growth type ght in San Pedro are outside the scatter for Pacific Northwest. This type was character- l by relatively steep slope, or slow rate of eleration, and small calculated ultimate size. interpreted this to mean that there was in n a large proportion of San Pedro 4-ring fish t would never have been caught in the Pacific rthwest. Likewise, a smaller proportion of nadian fish were outside the San Pedro scatter might never be caught in southern California. Scatter diagrams (fig. 7) of San Francisco =514, symbolized by x) and Monterey =783, symbol o) show many fish of the north- type. Numerous individuals from Monterey hes also fall within the scatter of character- ally San Pedro type (*cf.* fig. 6). San Fran- o shows few of the latter but a large propor- of types common to Canada; namely, with tively rapid deceleration rates and greater mptotic lengths.

These regressions of l_∞ on k for 1939-year-class hard caught in the 1943–44 season were vilinear as in the aquarium fish *Platypoecilus maculatus*, and some individuals with improbably high calculated asymptotes [2] were found as in platies (Felin 1951).

Similar regressions for individual pilchard of the same year class were plotted at the 6-ring stage (fig. 8). By this time, individuals of an unlikely predicted ultimate size were not represented in the catches anywhere along the Pacific coast and calculated asymptotes were well within the probable range of size for the species. As a result of the disappearance of these types, the regressions appear linear.

The scatter for 6-ring pilchard at all four ports included 194 individuals. Of these, 10 percent were entirely outside the main scatter of all fish. This group showed southern growth characteristics. Out of 70 from Canada only 1 percent were of this type with slow deceleration rate and low predicted size. Of 54 fish from San Francisco, 11 percent were of this type; of 57 in Monterey, 7 percent; and out of the small number, 13, of this older age caught at San Pedro, 62 percent had the typically southern growth characteristics.

The high percentage of these fish in San Pedro is in agreement with the appearance of predominantly southern-type annuli in San Pedro scales. Many scale samples taken from sardines off southern California and a few collected off Lower California show faint winter marks and wide zones of summer growth; the yearly increments decrease very slowly in size, illustrative of their slow deceleration in growth. (See figure 5b.) These fish are characteristically of small size for their age compared with northern types (see fig. 5a), and so far have not been observed to attain as great age as the large northern pilchard. Their position in this respect appears similar to that of the warm-water Mediterranean pilchard when compared with North Sea types (*cf.* fig. 2).

From the few available samples of Mexican fish taken off northern Lower California there is also indication of another southern growth type characterized by a low k value (the slope is even less than that for northern types), and by a small calculated ultimate size. (See figure 5b.)

The pilchard scales were photographed by means of infrared plates. This method was used by Roper (1936), to bring out year rings as distinct

[2] J. L. Hart (personal communication) recorded a standard length of 351 mm. for a pilchard caught off the west coast of Vancouver Island and landed at Nootka.

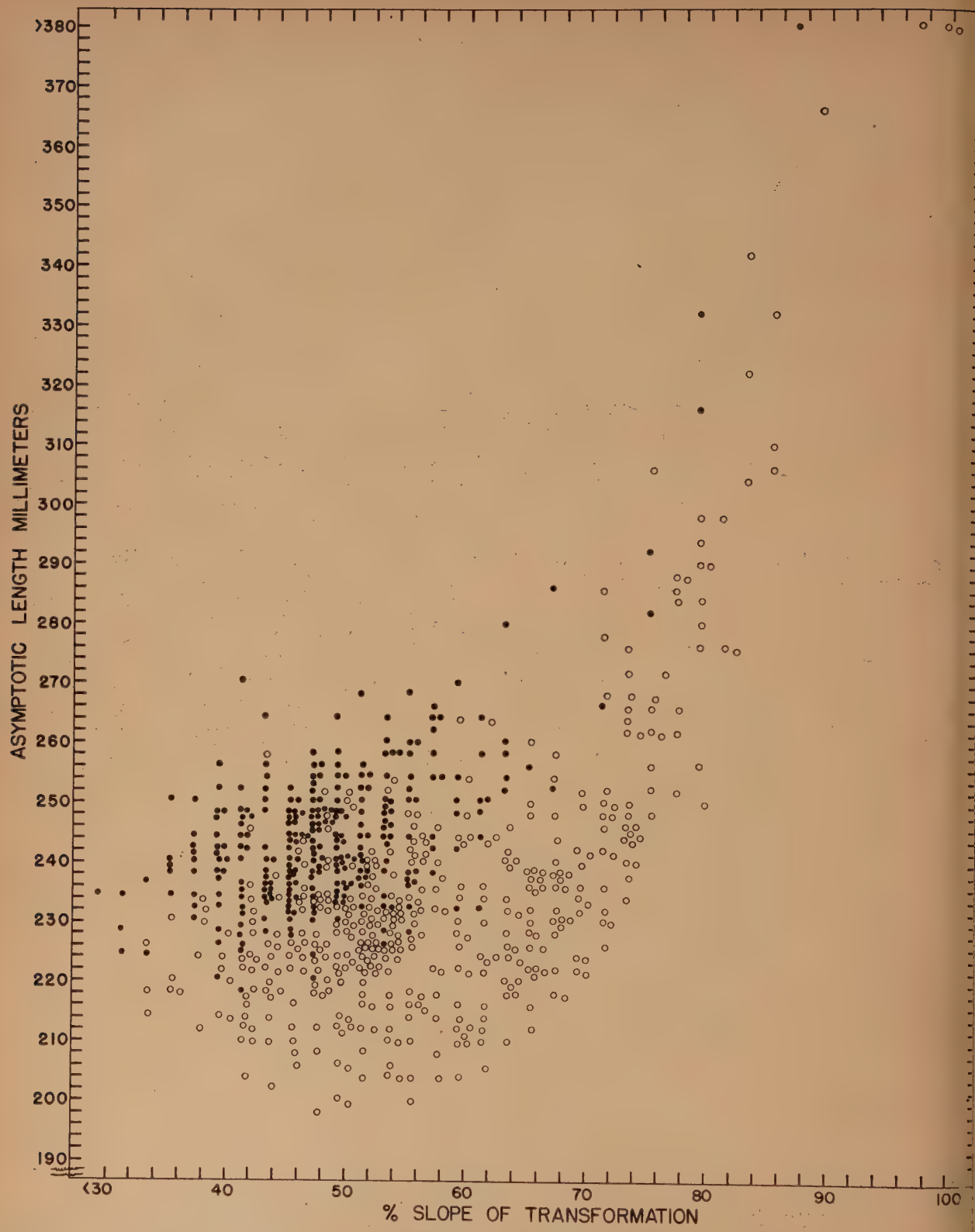
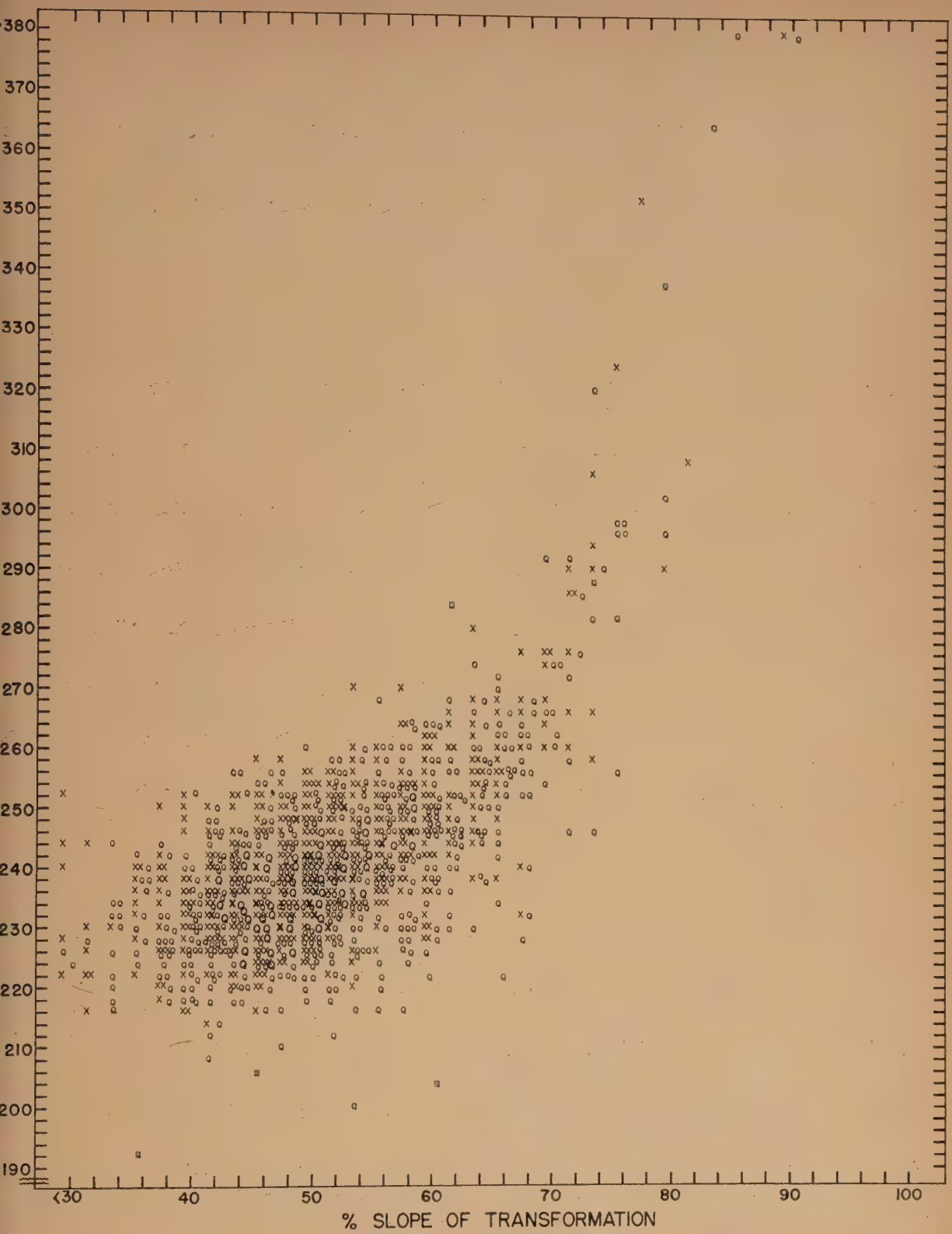


FIGURE 6.—Regression of transformation values calculated for individual pilchard of 1939 class caught at the 4-ring stage asymptotic length (l_∞) on rate of deceleration of growth (k). Dots represent fish taken in Canada, circles in San Pedro.



URE 7.--Regression of transformation values calculated for individual pilchard of 1939 class caught at the 4-ring stage, asymptotic length (l_∞) on rate of deceleration of growth (k). Symbol x represents fish taken in San Francisco, symbol o in Monterey. Larger symbols represent values for five fish, smaller for a single individual.

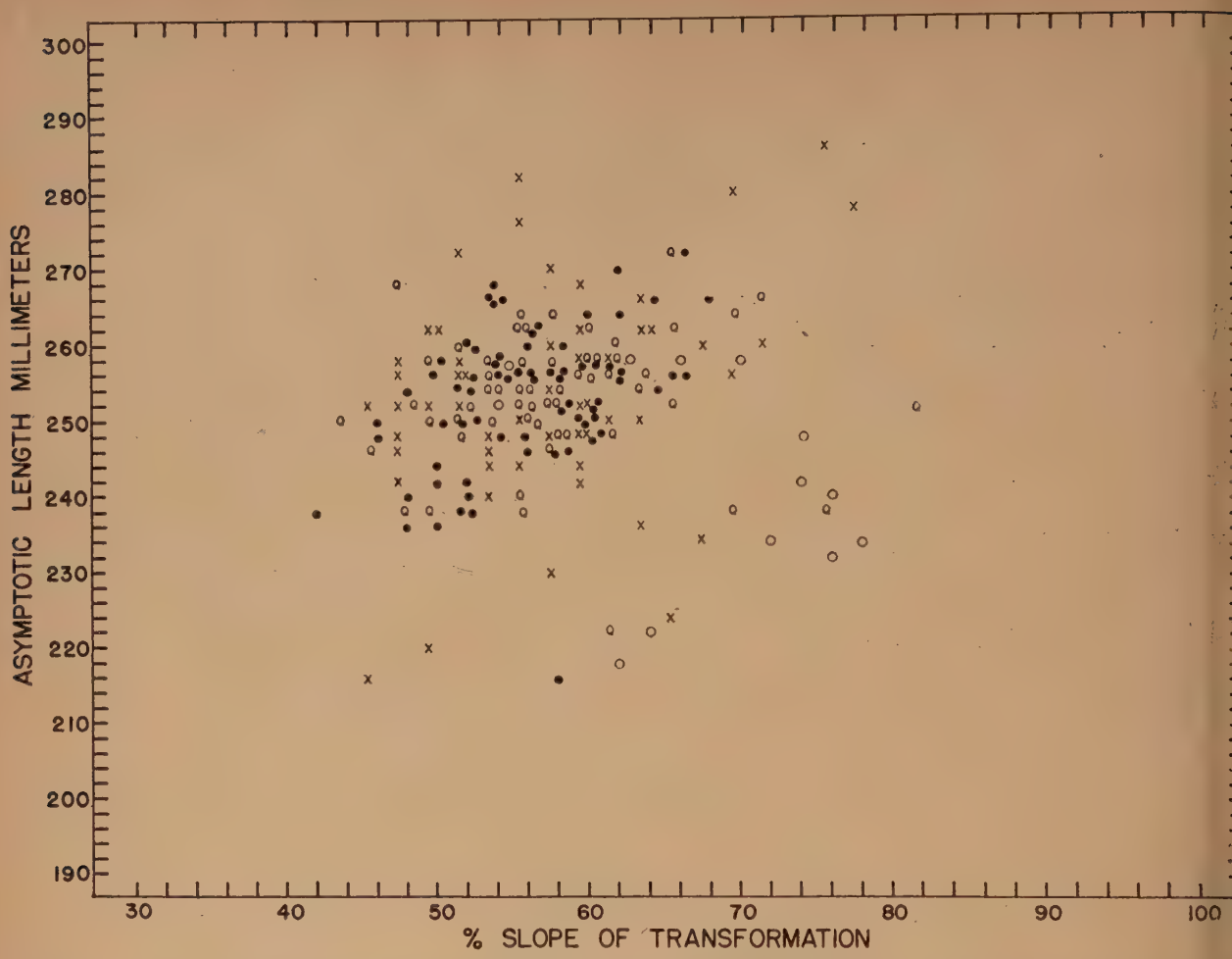


FIGURE 8.—Regression of transformation values calculated for individual pilchard of 1939-class caught at the 6-ri stage, asymptotic length (l_∞) on rate of deceleration of growth (k). Dots represent individuals taken in Canad circles San Pedro, symbol x San Francisco, symbol o Monterey.

from false rings in opercula of perch, and appears a satisfactory means of photographing pilchard scales.

Hessle (1925) gives illustrations of scale types which show differing growth patterns in various races of Baltic herring. The autumn-spawning herring which spawn in coastal waters (never inside archipelagoes) show rapid growth during the first 3 years and subsequent rapid falling off in growth increments. This is likewise the growth pattern of the somewhat smaller, spring-spawning sea herring of the Baltic in the same region. (The pattern corresponds to pilchard growth with a low k value, or rapid rate of deceleration in growth.) The fjord herring, on the other hand, also spring spawners, are sometimes quite isolated and show great variability in size with some dwarf and som giant forms. Hessle notes (p. 37) that "these tw herring forms [dwarf and giant] show a strikin similarity as regards actual mode of growth." H figures (p. 40) the "even growth" typical of a the fjord herrings as contrasted with the "stagnan growth" (pp. 17, 33) of sea herring of the Balti He also found (p. 45) ice herring in the Gulf Bothnia with a growth pattern and spawnin habits similar to the fjord herring. He conclude that—

> mode and rate of growth seems . . . to be very like th of the most rapid-growing fjord-herrings of the Mid Baltic. It is therefore natural to suppose that the spring-spawners of the Gulf . . . are closely related the fjord-herring of the Middle Baltic.

even-growth pattern of Hessle corresponds he southern growth type of the Pacific sardine a high k value, or slow deceleration in growth.

CONTRACTION OF FISHED STOCKS

Recent catch data may be pertinent also to the blem of populations. The abrupt decline in dings of pilchard in recent seasons reached a of 130,000 tons in 1947–48, the lowest in the ory of the fishery on the Pacific coast since 3–24 (Anonymous 1948). To account for decline, a number of explanations have been red by pilchard investigators, all of which y affect in varying degrees the fished popula-(s): (1) Lowered recruitment of young fish, reduced availability of fish to the fisherman, increased natural mortality, and (4) increased ing mortality.

The decline in catches in central California and he Pacific Northwest have been almost entirely onsible for the sudden decline in total catch he coast as a whole. In all these ports there been poor fishing since the 1945–46 season and the Northwest there were no landings during 1949 and 1950 seasons.

n southern California, however, the total ch did not fall off conspicuously up to 1950–51, in this season San Pedro recorded the largest nage of sardines ever taken there. The catch unit-of-effort did fall in 1947–48 (Clark and ugherty 1950, 1952), but for no other recent son has it differed greatly from previous aver-lunar months. Concentration of sardines on thern grounds has been used as argument by resentatives of the industry to obtain legal ension of Monterey grounds 70 miles to the th (Monterey Herald, May 14, 1951).

Contraction of areas of good fishing and ap-ent contraction of spawning areas may be endent on hydrographic changes, and center-of the available population in the southern of the range thus may have produced a es of southern year classes.

DISTINGUISHING SOUTHERN AND NORTHERN YEAR CLASSES

o detect early in its life in the fishery a year s that is likely to be primarily southern, some measure of its relative strength in northern and southern areas of catch is desirable. One measure of strength of a year class in the fishery has been the numbers of pilchard in the 3-ring stage caught at all ports (Walford 1946b). Although availability and degree of recruitment at earlier ages are more variable, another measure of early strength of a year class in any region is the number of 1-ring or 2-ring fish caught at any port. At this age presumably, migrating pelagic sardines would be less widely dispersed throughout their possible habitat and nearer their point of origin.

San Pedro is considered the port nearest centers of spawning. Early strength of a year class at this port may be taken as a measure of spawning success in the south. Figure 9 shows ratios of catch per boat-month (using California catch-per-unit data, Clark and Daugherty 1950) at San Pedro to catch per boat-month [3] for the coast as a whole for 1-ring (dot) and 2-ring (circle) sardines of each year class over the period of comparable sampling (1941–49). The year-class strength for the Pacific coast as measured by catch per boat-month at the 3-ring stage is also figured (symbol x). (There is rather close correspondence between year-class strength at 2-ring and at 3-ring. For the 1947 year class, the number caught at 2-ring is figured, by symbol +, as an approximation of its probable strength in the following season.)

When the ratio of San Pedro 2-ring fish to the Pacific-coast total was low, as in the 1939 year class, the total year-class strength for the whole coast was well above average. The 1940 year class was slightly above average strength; the ratio San Pedro to Pacific coast was somewhat above 1.0 at 1-ring, somewhat greater at 2-ring. The 2-ring age group usually dominates at San Pedro. The 1941 class, however, was the dominant age group as 3-ring at San Pedro in 1944–45, showed a high ratio to the rest of the coast, was somewhat below average in year-class strength, and was relatively below normal numbers in northern ports throughout its life in the fishery. By these criteria, the 1939 year class may be called a successful year class with early strength in the northern fishery, the 1941 class relatively

[3] When estimates of total numbers of sardines caught, by year class, are used instead of those adjusted for fishing effort the results correspond closely.

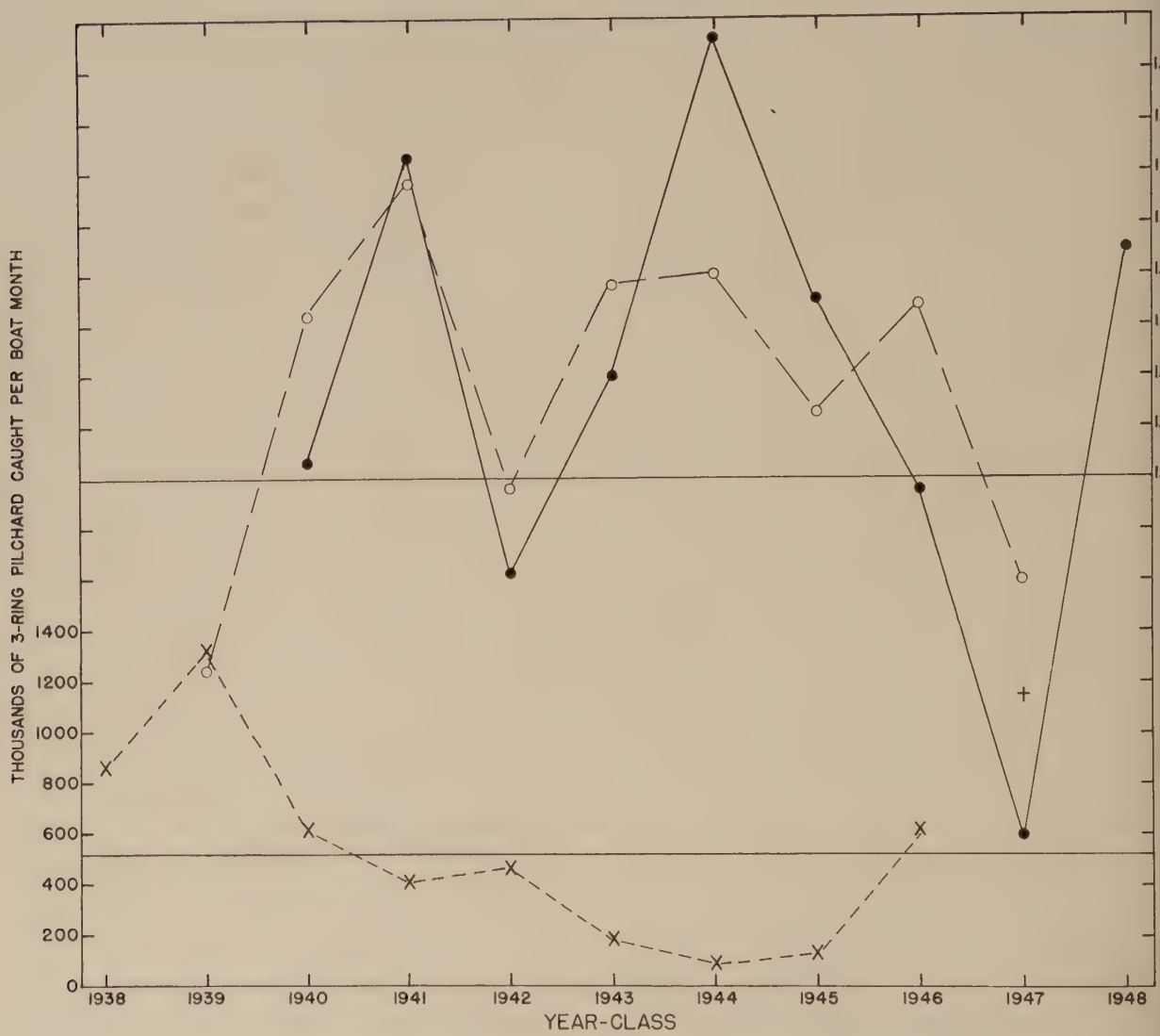


FIGURE 9.—Ratios of numbers of pilchard of each year class taken per unit-of-effort at San Pedro to those taken alo the whole Pacific coast as 1-ring (dot), as 2-ring (circle). Numbers of fish of each year class taken per unit-of-effo at the 3-ring stage are shown (symbol x) as relative measures of year-class strength.

s successful and primarily a southern year class.[4] e 1942 class was of about average strength and San Pedro-Pacific coast ratio indicated prob- e northern origin. The year classes 1943, 4, and 1945 were below average strength and wed early dominance at San Pedro as com- ed with the rest of the coast. The 1946 year ss was above average strength and the San dro-Pacific coast ratio was below 1.0 at 1-ring, nough comparatively in greater numbers as ing at San Pedro. The 1947 class appears the st successful of any year class since that of 9, and it shows a low San Pedro-Pacific coast io.

From these data the existence of southern and thern year classes seems indicated. Early thern strength, or a low ratio, may prove indic- ve of a widespread spawning and a relatively cessful year class. There also are indications t a strong southern year class, such as those of 1, 1946, and probably 1948, can make such nificant contributions to southern catches that ir year-class strength when measured by num- s caught along the whole coast at 3-ring still be considerable. It is nevertheless only se year classes 1943, 1944, and 1945 which ear predominantly southern, by these criteria, t so far have been much below normal strength. The San Pedro to Pacific coast ratios at 1-ring y be a better measure of relative year-class ength by region than ratios at 2-ring. There apparent wide variations in availability, as l as in recruitment, of pilchard at 1-ring as wn in total numbers of this age class caught ing each season at each port (*cf.* Felin and llips 1948: Mosher et al. 1949; Felin et al. 9; Felin et al. 1950; Felin et al. 1951). Such le variations are likely to be associated with origins of each year class. By the time sar- es have reached 2-ring they may be more ely dispersed and their origins more obscure. rt (1943a, p. 174), for example, noted that two fish, probably of the 1939 year class, tagged at Monterey by the California Bureau of Marine Fisheries, were taken off the Canadian coast early in 1941, presumably at the 2-ring stage.

In general, the assumption that 1- and 2-ring fish have not traveled great distances is substantiated by the behavior of tagged sardines of these approximate sizes. Data from Janssen (1938) and Clark and Janssen (1945) show that recoveries to the north of fish from the southern California tagging area are at first of larger sizes than commonly would occur in the 1- and 2-ring age classes. It is also evident from Phillips' (1948, p. 7) average length-on-time growth curves for the Pacific Northwest, central California, and southern California, that for the 6-season period (somewhat subsequent to the tagging data) the mean observed lengths at 1- and 2-ring are greater for San Pedro fish than for those caught in the Pacific Northwest. In central California, 1-ring fish average smaller than those in the other two areas. At 2-ring, central California sardines begin to exceed the sizes at San Pedro. At 3-ring the sizes of Pacific Northwest pilchard begin to exceed those caught in the other two areas. These data indicate that few large 1- and 2-ring fish have left the southern California area.

Further evidence that the larger 1-ring and 2-ring sardines have not migrated far from the southern grounds is provided by calculated length data (table 4). At 1-ring the mean calculated first growth increment, $\bar{l}_1$, is greater at San Pedro than at Monterey for all the year classes over the 9-year period of study. At 2-ring, for nearly all year classes the $\bar{l}_1$ still is greater in the southern area. By the time the year classes have reached 3-ring the situation has reversed and the calculated first growth increments are nearly all greater in central California, indicating a strong influx of southern fish with large $\bar{l}_1$ into the area. For nearly all year classes at 4- and 5-rings of age the average calculated first growth increment continues to be greater at Monterey than at San Pedro.

Ronquillo (1949, p. 12) found statistically significant difference in mean observed lengths of 0- and 1-ring fish in San Pedro and Monterey and concluded that "fish reared in these two areas do not intermingle at this age." Since the commercial fishery is carried on in the winter off California when growth is minimal and the first ring will soon

[4] William T. Miller (ms.) found that temperature conditions in the spring 1941 were unusually warm in the area off Lower California during February March, and that according to United States Hydrographic Office records, r temperatures were higher than those normally associated with pilchard ning. His charts suggest that during this season temperatures favor- for spawning were restricted both in space and time, namely to the area outhern California. He contrasted the 1941 season with the 1939, an ually cold spring, and showed that during the latter season temperatures ower California were favorable for spawning over a wide area in Febru- March, and April. Water temperatures suitable for the widespread ern spawning known to have taken place in 1939 were also recorded. relative scarcity of fish of the 1941 year class in northern catches might be attributed to contraction of areas and time of spawning.

TABLE 4.—*Calculated mean first growth increments* ($\bar{l}_1$) *for pilchard year classes from 1- to 5-ring caught at San Pedro and Monterey, 1936–48*

Year class	1-ring				2-ring				3-ring				4-ring				5-ring			
	San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monter	
	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	
1936																	47	104	42	
1937													160	105	193	107	53	102	159	
1938									1, 169	98	1, 054	100	453	96	672	101	100	98	351	
1939					1, 707	93	2, 512	94	1, 293	92	1, 581	95	424	96	1, 146	97	174	98	534	
1940	256	121	313	118	1, 287	109	554	107	807	106	934	110	413	103	470	108	44	105	71	
1941	332	115	69	98	1, 069	103	253	100	1, 134	98	350	103	151	100	153	101	26	107	43	
1942	386	108	563	96	1, 042	98	1, 376	96	242	102	319	103	60	116	81	109	46	109		
1943	523	105	446	104	335	101	254	107	189	107	140	115	83	115			10	116		
1944	106	114	74	107	259	128	96	110	161	126			33	133			27	130	30	
1945	370	143	327	117	281	139	100	99	99	131	23	114	60	133	62	132				
1946	195	109	357	107	407	112	59	103	209	117	172	116								
1947	59	123	613	104	242	121	503	101												
1948	71	140	14	133																

appear, the observed length at 0-ring is comparable to the calculated length at 1-ring, and observed length of 1-ring fish is comparable to the calculated length at 2-ring.

Tagging and growth data thus both appear to indicate a tendency for larger fish to migrate farther north, but there is apparently not a great deal of emigration of the large 1- and 2-ring sardines from the southern California grounds so that these early ages may be used as reasonably good indices of early year-class strength in one geographical area.

ANOMALIES IN YEAR-CLASS CATCH CURVES

Vital statistics of the fishery show that new sources of fish were unexpectedly available in season 1949–50 (Felin, Daugherty, and Pinkas, 1950 and 1951). The overavailability of certain ages is reflected in certain anomalies in year-class catch curves at all California ports. At all three ports there was a marked deviation from the previous trend of total mortality rate for 1944 and 1945 year classes, as 4- and 5-ring fish. In central California ports, the 1943 and 1946 year classes also showed increase in availability (as defined by Marr 1951).

BIMODALITY IN LENGTH-FREQUENCY COMPOSITION

There are also indications of bimodality in length-frequency composition of the 1944 year class caught during the 1949–50 season in California ports (Felin, Daugherty, and Pinkas, 195

Study of growth transformations from calculat lengths of individual fish of the 1944 year cla showed that coincident with the unexpected large catches of this year class as 5-ring fish 1949–50 there were many small-sized individua of this age caught in San Pedro and Montere Some of these 5-ring fish were smaller than sa dines of the same year class as 4-ring so that the presence in the catches could not be account for as small fish remaining after the exodus larger migrants going north. Their presence mu rather be explained as an influx, probably from t south, of small fish into the southern and centr California fishing areas. That this appears to a strongly southern year class is indicated in figu 9. The average observed lengths of the 1944 ye class as 5-ring at San Pedro and Monterey al show a decrease as compared with the same ye class caught as 4-ring fish in the previous seaso

An appearance of bimodality has also be observed in the length composition of other ye classes in previous seasons (*cf.* Felin and Phill 1948), and is further evidence from growth th pilchard caught along the Pacific coast do n constitute a single homogeneous population.

SUMMARY AND CONCLUSIONS

1. The question whether the fished stocks the Pacific pilchard, or sardine, along the Paci coast are homogeneous is considered in the lig of evidence from growth studies and other vit statistics.

. The direct proportionality of growth of le to growth of fish is used to obtain approxi- tions of mean calculated lengths of sardines.
. Walford's (1946a) transformation plot is plied to mean observed length data and mean culated length data sampled in different ions.
. Comparison is made of growth character- cs, k (slope of the regression, or rate of decelera- n of growth) and l_∞ $\left(\frac{y-\text{intercept}}{1-k}, \text{ or calculated ultimate size}\right)$ of six year classes sampled the most northern region of catch, Canada, l the most southern, San Pedro.
. From analysis of covariance no significant ferences are evidenced in the mean slopes, k, the transformations between each of these six ar-classes in Canada and San Pedro.
. For each year class tested, two distinct ntercepts, or levels, of mean transformations maintained in the northern and southern as, and from the covariance tests the differ- es are significant at the 1-percent level. The wth characteristic l_∞ thus differs significantly he northern and southern catches.
. The use of the straight-line transformation a method of expressing growth differences not dily apparent in conventional length-on-time wth curves was noted by Walford (1946a). e applicability of the usual statistical tests of nificance to such regressions of l_{n+1} on l_n is now apparent. Possible meanings of significant ference in k and l_∞ as physiological characters discussed.
. Complete intermixture and homogeneity in pulations of adult fish as sampled by the fishery different regions is not evidenced from data on an calculated lengths.
. The apparent cline in the growth charac- stic l_∞ appears indicative of intraspecific pulations in which there is limited intermingling, suggests a series of overlapping coastal grations of more than one stock.
0. The recent discovery of an area of intense wning off central Lower California, more or discrete from the widespread spawning area southern California, points to the tentative othesis that spawning grounds off Lower California give rise to the southern components found in catches off San Pedro (and to a lesser degree off central California), while the larger fish originate off southern California and occasionally to the north.

11. Evidence from qualitative and quantitative differences in individual scale and growth patterns indicates some independence in the fished stock of the Pacific Northwest and southern California.

12. The decline in catches in central California and the Pacific Northwest has been almost entirely responsible for the sudden decline in total catch of the entire coast. It is suggested that the centering of the available population in the southern part of the range may have produced a series of southern year classes.

13. Ratios between year-class strength of 1- or possibly 2-ring fish taken at San Pedro and taken along the coast as a whole may prove a useful index in determining whether a year class is primarily southern or has more northern components.

14. The measure of year-class strength used by Walford (1946b), i. e., the number of 3-ring pilchard caught at all ports, is compared with the San Pedro–Pacific coast ratios of 1- and 2-ring fish. To date only those year classes which appear predominantly southern by these criteria have been much below normal strength.

15. Vital statistics of the fishery which indicated that new sources of fish became unexpectedly available in the 1949–50 season appear to be explained at least in part by an influx, probably from the south, of small fish onto the southern and central California fishing grounds.

16. Bimodality in length-frequency composition is further evidence from growth that pilchard caught along the Pacific coast do not constitute a homogeneous population.

17. Whether heterogeneity in growth characteristics is the expression of genotypic difference or a phenotypic response of a species to its environment is not yet determined.

18. In view of differences in stocks on the various fishing grounds along the Pacific coast, the study of population dynamics not only for the coast as a whole but also by geographic areas appears desirable.

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